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Out of Africa: origins of the *Taenia* tapeworms in humans

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Phylogenetic and divergence date analyses indicate that the occurrence of *Taenia* tapeworms in humans pre-dates the development of agriculture, animal husbandry and domestication of cattle (*Bos* spp.) or swine (*Sus scrofa*). Taeniid tapeworms in Africa twice independently colonized hominids and the genus *Homo* prior to the origin of modern humans. Dietary and behavioural shifts, from herbivory to scavenging and carnivory, as early *Homo* entered the carnivore guild in the Pliocene/Pleistocene, were drivers for host switching by tapeworms to hominids from carnivores including hyaenids and felids. Parasitological data provide a unique means of elucidating the historical ecology, foraging behaviour and food habits of hominids during the diversification of *Homo* spp.

Keywords: *Taenia* tapeworms; human parasites; evolution; historical ecology

1. INTRODUCTION

Taeniid tapeworms, the focus of exhaustive taxonomic and epidemiological studies, have a global economic impact through morbidity and mortality in humans and production losses in domestic stock (Abuladze 1964; Verster 1969; Rausch 1997). Species of taeniid tapeworms that are host specific in humans, *Taenia saginata*, *T. asiatica* and *T. solium*, have synanthropic life cycles dependent on domesticated ruminants as intermediate hosts (Eom & Rim 1993; Fan & Chung 1995; Rausch 1997). Occurrence of these cestodes in humans has traditionally most often been linked to the domestication of obligatory intermediate hosts such as cattle (*Bos* spp.) and swine (*Sus scrofa*) and coincidental colonization of humans by cestodes typical of companion carnivores such as dogs, not more than 10 000 years ago (Baer 1940; Cameron 1956). Here we present phylogenetic evidence that contradicts this hypothesis and indicates that hominids, on the savannah of Africa, became hosts for *Taenia* prior to the origin of modern humans and substantially earlier than the domestication of bovids and suids and the development of agriculture. Our analyses indicate that African hominids that scavenged or preyed upon antelope and other bovids were exposed to colonization by *Taenia* tapeworms that were using hyaenids, canids and felids as definitive hosts and bovids as intermediate hosts. Species of *Taenia* are historical ecological indicators of the foraging behaviour and food habits of hominids during the diversification of *Homo* spp.

Taeniid tapeworms in their adult stage are characteristic parasites in carnivorous mammals. The host-specific taeniids of humans have life-history patterns typical of Taeniidae in general, in which a carnivore is the definitive host and a herbivore is the intermediate host (Rausch 1997; Loos-Frank 2000). In the case of human-parasitic *Taenia*, cattle are now the obligatory intermediate hosts for *T. saginata*, whereas swine serve this role for *T. asiatica* and *T. solium* (Abuladze 1964; Eom & Rim 1993). Intermediate hosts ingest eggs of *Taenia* that develop into cysticercus larvae in the body of the host. The cestode life cycles are completed when under-cooked meat or visceral organs, such as the liver, infected by cysticercus larvae are consumed by humans.

Phylogenetic analyses of *Taenia* spp. permit examination of the historical relationships of species restricted to human definitive hosts (e.g. Brooks & McLennan 1991). These analyses indicate that species of *Taenia* in humans do not form a clade (*T. saginata* and *T. asiatica* are putative sister species, unrelated to *T. solium*) and may represent two independent shifts to hominid hosts (De Queiroz & Alkire 1998; Hoberg *et al.* 2000). Additionally, parsimony reconstructions of host associations and geographical range are consistent with the idea that the immediate ancestors of both lineages of human-parasitic *Taenia* lived in Africa and had carnivores and bovids (but not *Bos*) as definitive and intermediate hosts, respectively. Thus, hominids were independently colonized by tapeworms of carnivores in Africa. This pattern is consistent with evolution among other *Taenia* spp., where diversification has been linked primarily to colonization of carnivorous definitive hosts, rather than to host switches between herbivorous intermediate hosts (Hoberg *et al.* 2000).

The African ancestry of human-parasitic *Taenia* is critical in comparing the hypothesis that hominids acquired these tapeworms before cattle and pigs with the traditional idea that humans acquired *Taenia* coincidental with the domestication of these typical intermediate hosts. Neither hominids nor these domestic animals (or congeneric species) are parasitized by close relatives of human-parasitic *Taenia* (table 1), and so both hypotheses require the same number of host shifts. The 'hominids first' hypothesis, however, provides a better explanation of how tapeworms circulating among carnivores and antelope in Africa could have colonized a novel definitive host. Specifically, there is now compelling evidence that the African ancestors of modern humans fed on bovids (De Heinzelin *et al.* 1999; Sponheimer & Lee-Thorp

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Table 1. *Primary definitive and intermediate hosts for species in the* Taenia solium *and* T. saginata *subclades, and a context for diversity in carnivore palaeoguilds and among potential bovid prey*

species	definitive host	intermediate host
T. solium sub-clade		
T. solium	*Homo sapiens*	*Sus scrofa*
		Potamochoerus porcus[a]
		Homo sapiens, primates[a]
		Lagomorpha[a]
		Canidae[a]
		Procaviidae[a]
T. hyaenae	*Hyaena brunnea*[b]	*Aepyceros melampus*[c]
	Crocuta crocuta[b]	*Hippotragus niger*[c]
	Lycaon pictus	
T. crocutae	*Hyaena brunnea*[b]	*Aepyceros melampus*[c]
	Crocuta crocuta[b]	*Connochaetes taurinus*[c]
		Damaliscus lunatus[c]
		Hippotragus equinus[c]
		Hippotragus niger[c]
		Tragelaphus strepsiceros[c]
		Sylvicapra grimmia
		Syncerus caffer[c]
		Kobus leche[c]
T. gonyamai	*Panthera leo*[b]	*Aepyceros melampus*[c]
	Acinonyx jubatus[b]	*Connochaetes taurinus*[c]
		Syncerus caffer[c]
		Tragelaphus strepsiceros[c]
T. madoquae	*Canis mesomelas*[b]	*Madoquae guentheri*[c]
T. saginata sub-clade		
T. saginata	*Homo sapiens*	*Bos* spp.
T. asiatica	*Homo sapiens*	*Sus scrofa*
		Bos taurus[a]
T. simbae	*Panthera leo*[b]	antelopes[c]

[a] Secondary intermediate host.
[b] Genus or species of carnivore represented as a component of the large carnivore guild in Africa during the Pliocene/Pleistocene (Lewis 1997).
[c] Genus or species of potential bovid prey for carnivores and hominids in the carnivore guild (Vrba 1985; De Heinzelin *et al.* 1999).

1999), thus providing the opportunity for tapeworms circulating among a paleoguild of carnivores and herbivores to colonize Pliocene or Pleistocene hominids. In contrast, there is no evidence that the recent ancestors of domestic cattle or swine even occurred in sub-Saharan Africa (K. Behrensmeyer, personal communication; from the Smithsonian Institution Evolution of Terrestrial Ecosystems database). The examination of these hypotheses is the focus of this investigation.

2. MATERIAL AND METHODS

(a) *Phylogeny and host–parasite associations*

This study is based in part on initial analyses of *Taenia* phylogeny presented by De Queiroz & Alkire (1998) and Hoberg *et al.* (2000). For this study, 35 species of *Taenia* were included in phylogenetic analyses based on the matrix of 28 characters, derived from comparative morphology, presented in Hoberg *et al.* (2000); character 28, the presence of exogenous larval proliferation, is apomorphic in *T. polyacantha* and *T. crassiceps*. This contrasts with the original study by Hoberg *et al.* (2000) in which 30 species were included in the analysis, thus allowing a more complete examination of tree topology. Although Loos-Frank (2000) lists 44 species and subspecies in *Taenia*, this analysis excludes subspecies ($n=4$), species based only on metacestodes ($n=3$) and two species, *T. krepkogorski* and *T. jaipurensis*, that could not be studied in detail.

Parsimony analyses were conducted with PAUP 3.1.1 (Swofford 1993), using heuristic searches, random addition sequence (50 repetitions) and branch swapping by tree bisection–reconnection (see also Hoberg *et al.* 2000). Tree space was further explored through analyses using random addition and variation in options for branch swapping. Consensus trees (50% majority rule) were used to examine relationships in instances where multiple equal-length trees resulted from the analyses.

Host–parasite relationships, biogeography and putative historical associations were examined by mapping extant host taxa (family level) onto the parasite tree. This was accomplished by using separate matrices for intermediate and definitive hosts and geography, and optimizing these characters on the parasite phylogeny with MacClade 3.08 (Maddison & Maddison 1992). Data for life-history and host associations are derived primarily from summaries in Verster (1969) and Loos-Frank (2000).

(b) *Estimates for dates of divergence*

If one assumes the minimum number of host shifts then the common ancestor of *T. saginata* and *T. asiatica* was already a parasite of humans. Under this assumption, an estimate of the divergence date between these two species is also an estimate of the most recent date for colonization of humans by the common ancestor of these *Taenia* species.

We estimated the date of divergence between *T. saginata* and *T. asiatica* using cytochrome *c* oxidase I (COI) sequences from Bowles & McManus (1994). Rates of base substitution in COI can vary substantially across lineages (e.g. Martin *et al.* 1992; Hafner *et al.* 1994) and the rate has not been calibrated for *Taenia* (nor, for that matter, in any other platyhelminth). Here, we assume that the substitution rate in *Taenia* falls within the range of substitution rates estimated for organisms for which rates can be calibrated using fossil or other geological evidence.

We limited comparisons to relatively recently diverged taxa (< 10 million years (Myr)) for which there is either a relatively good fossil record (*Homo–Pan*, *Mus–Rattus*) or strong geological evidence dating a vicariance event (*Alpheus*, *Sesarma*, *Sphyrna*). Calibrated substitution rates also exist for more distant splits but these estimates are more sensitive to violations of the substitution model than are estimates from relatively recent divergences.

Nearly all differences between *T. saginata* and *T. asiatica* are at third positions, thus, we limited comparisons to third positions. All of the comparisons we used show a higher frequency of transitions than transversions, thus, we took this difference into account in estimating substitution rates, using the method of Kimura (1980) as described in Li & Graur (1991). The results are qualitatively similar, however, if transition–transversion differences are ignored.

For any of the calibrated divergence dates, if a range of dates was given in the literature, we used the most recent date. This results in faster estimated substitution rates and is thus conservative with respect to our hypothesis that the *T. saginata–T. asiatica* split pre-dates the domestication of ungulates. In the original study of snapping shrimp (*Alpheus*), several different pairs of taxa were used. Out of these, we used only the most genetically divergent pair, which is also the most conservative approach with respect to our hypothesis.

The calculations of divergence dates assume a constant rate of substitution. We performed relative-rate tests for *T. saginata* and *T. asiatica* using the method of Steel *et al.* (1996) to test the null hypothesis that the rate of substitution is constant. With either *T. multiceps* or *T. ovis* as the reference taxon, the test failed to reject the null hypothesis.

3. RESULTS

(a) Taenia *phylogeny and host relationships*

Parsimony analysis resulted in 124 equal-length trees (194 steps, consistency index = 0.253, homoplasy index = 0.747); relationships are similar to but less resolved than those depicted in Hoberg *et al.* (2000) (figure 1). The shortest trees were recovered by analyses using tree bisection–reconnection and random addition sequences. Consistent with prior phylogenetic studies of *Taenia*, the three species *T. solium*, *T. saginata* and *T. asiatica* do not form a clade, although *T. saginata* and *T. asiatica* are sister species. Within the context of this study, sub-clades that contain species of parasites in human-definitive hosts are similar to those recovered in previous analyses based on a smaller subset of taxa and comparative morphology. Alternative topologies relative to those species in human-definitive hosts were not recovered in these analyses.

Species of *Taenia* in human-definitive hosts can be divided into two sub-clades: the '*T. solium* sub-clade' containing *T. solium*, *T. hyaenae*, *T. crocutae*, *T. gonyamai* and *T. madoquae*, and the '*T. saginata* sub-clade' including *T. saginata* and its sister species, *T. asiatica*, and *T. simbae*. We examined relationships between *Taenia* spp. and definitive hosts (figure 1*a*), primary intermediate hosts (figure 1*b*) and geographical range (figure 1*c*) by parsimony optimization of these characters on the parasite phylogeny. Morphological phylogenies in this study and from Hoberg *et al.* (2000) and a more limited molecular phylogeny (De Queiroz & Alkire 1998) indicate that *T. saginata* + *T. asiatica* and *T. solium* represent the result of two independent host shifts to hominids. For both groups, phylogenetic analyses are consistent with the hypothesis that the immediate ancestors of these tapeworms used carnivores (hyaenids, canids or felids) as definitive hosts and bovids as intermediate hosts, and that host switching occurred in sub-Saharan Africa. For *T. solium*, the most parsimonious reconstructions of host association (figure 1*a*,*b*) indicate that the most recent common ancestor of this species and its closest living relative, *T. hyaenae*, used hyaenids as definitive hosts (figure 1*a*) and bovids (but not *Bos* spp.) as intermediate hosts (figure 1*b*). Parsimony mapping unequivocally indicates that this ancestor was an African species (figure 1*c*).

For *T. saginata* + *T. asiatica*, parsimony reconstructions indicate that the most recent common ancestor of these species and their closest relative, *T. simbae*, used felids as definitive hosts (figure 1*a*) and bovids (once again not *Bos* spp.) as intermediate hosts (figure 1*b*). Parsimony mapping of geographical range does not unequivocally identify Africa as the range for this ancestral species; one of the most parsimonious reconstructions, however, places this ancestor in Africa. Additionally, cosmopolitan distributions for *T. solium* and *T. saginata* would have been acquired secondarily, coincidental with transcontinental movements of humans and their domestic stock, particularly after the 1500s.

(b) *Divergence dates for* T. saginata *and* T. asiatica

Point estimates for the divergence of *T. saginata* and *T. asiatica* range from *ca.* 0.78–1.71 Myr (table 2). In addition, we obtained 95% confidence intervals for the *T. saginata*–*T. asiatica* divergence, taking into account the sampling error for both the *Taenia* comparison and each calibrated comparison in turn, using the approach of Steel *et al.* (1996). The most recent 95% limit obtained from any of these analyses is 0.16 Myr (using *Alpheus*).

4. DISCUSSION

Phylogenies for species of *Taenia* in this study and from Hoberg *et al.* (2000) and a more limited molecular phylogeny by De Queiroz & Alkire (1998) indicate that *T. saginata* + *T. asiatica* and *T. solium* represent the result of two independent host shifts to hominids. For both groups, phylogenetic analyses are consistent with the hypothesis that the immediate ancestors of these tapeworms used carnivores (hyaenids, canids or felids) as definitive hosts and bovids as intermediate hosts, and that host switching occurred in sub-Saharan Africa prior to the domestication of ungulates (figure 1).

(a) *Divergence dates for* T. saginata *and* T. asiatica

The domestication of cattle and swine is thought to have begun about 10 000 years ago (Bradley *et al.* 1996; Epstein & Bichard 1984). Thus, the divergence-date analyses indicate that the *T. saginata* + *T. asiatica* lineage colonized humans well before the domestication of bovids or suids. This is true even if one takes the extremely conservative approach of accepting the most recent 95% confidence limit as the divergence date (0.16 Myr ago).

If one assumes the minimum number of host shifts, the common ancestor of *T. saginata* and *T. asiatica* was already a parasite of *Homo*. The above analyses suggest that the *T. saginata* and *T. asiatica* lineages diverged well before humans domesticated cattle and pigs. Thus, this evidence suggests that *Taenia* became associated with *Homo*, and later used humans as typical definitive hosts.

Several caveats should be kept in mind. First, the date of COI sequence divergence may not correspond to the date of species divergence. Specifically, if substantially different COI sequences were present within the ancestor of *T. saginata* and *T. asiatica* then it is possible that the divergence we are estimating substantially pre-dates the species divergence. Bowles & McManus (1994), however, found no sequence divergence among three isolates of *T. saginata* and among six isolates of *T. asiatica*. If the most recent common ancestor of these two species was similarly monomorphic then the current sequence difference between them should reflect the divergence of their lineages.

Second, *T. saginata* and *T. asiatica* could have much faster rates of substitution than any of the organisms we used to obtain substitution rates. Rates of synonymous substitution in chewing lice (*Geomydoecus*) are estimated to be between 3 and 11 times faster than those of their pocket-gopher (*Orthogeomys*) hosts (Hafner *et al.* 1994; Page 1996; Huelsenbeck *et al.* 1997). Assuming that the pocket gophers have rates of substitution similar to *Mus*

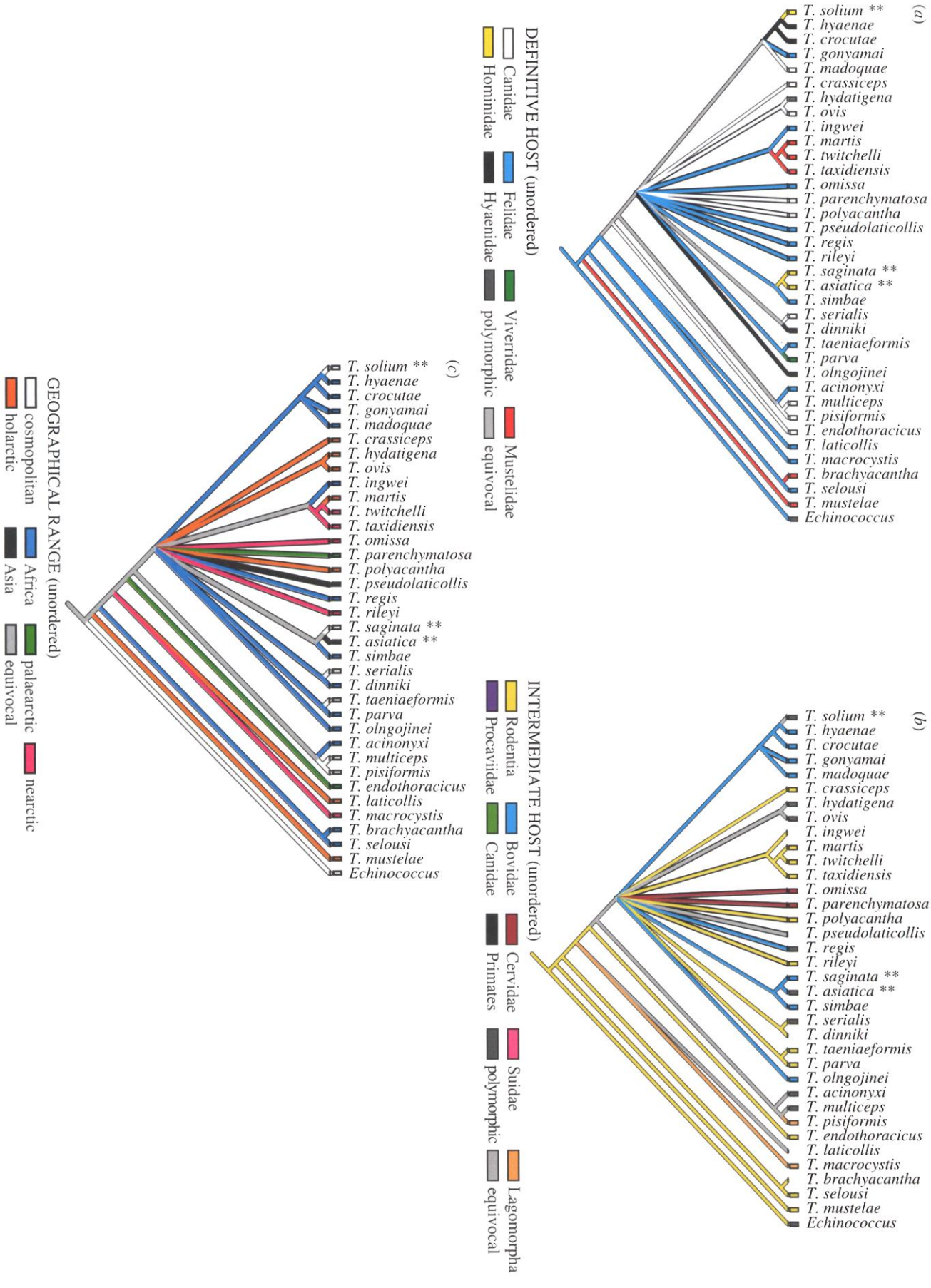
(a)
T. solium **
T. hyaenae
T. crocutae
T. gonyamai
T. madoquae
T. crassiceps
T. hydatigena
T. ovis
T. ingwei
T. martis
T. twitchelli
T. taxidiensis
T. omissa
T. parenchymatosa
T. polyacantha
T. pseudolaticollis
T. regis
T. rileyi
T. saginata **
T. asiatica **
T. simbae
T. serialis
T. dinniki
T. taeniaeformis
T. parva
T. olngojinei
T. acinonyxi
T. multiceps
T. pisiformis
T. endothoracicus
T. laticollis
T. macrocystis
T. brachyacantha
T. selousi
T. mustelae
Echinococcus
DEFINITIVE HOST (unordered)
Canidae
Felidae
Hominidae
Hyaenidae
Viverridae
Mustelidae
polymorphic
equivocal
(b)
T. solium **
T. hyaenae
T. crocutae
T. gonyamai
T. madoquae
T. crassiceps
T. hydatigena
T. ovis
T. ingwei
T. martis
T. twitchelli
T. taxidiensis
T. omissa
T. parenchymatosa
T. polyacantha
T. pseudolaticollis
T. regis
T. rileyi
T. saginata **
T. asiatica **
T. simbae
T. serialis
T. dinniki
T. taeniaeformis
T. parva
T. olngojinei
T. acinonyxi
T. multiceps
T. pisiformis
T. endothoracicus
T. laticollis
T. macrocystis
T. brachyacantha
T. selousi
T. mustelae
Echinococcus
INTERMEDIATE HOST (unordered)
Procaviidae
Rodentia
Canidae
Bovidae
Primates
Cervidae
polymorphic
Suidae
equivocal
Lagomorpha
(c)
T. solium **
T. hyaenae
T. crocutae
T. gonyamai
T. madoquae
T. crassiceps
T. hydatigena
T. ovis
T. ingwei
T. martis
T. twitchelli
T. taxidiensis
T. omissa
T. parenchymatosa
T. polyacantha
T. pseudolaticollis
T. regis
T. rileyi
T. saginata **
T. asiatica **
T. simbae
T. serialis
T. dinniki
T. taeniaeformis
T. parva
T. olngojinei
T. acinonyxi
T. multiceps
T. pisiformis
T. endothoracicus
T. laticollis
T. macrocystis
T. brachyacantha
T. selousi
T. mustelae
Echinococcus
GEOGRAPHICAL RANGE (unordered)
cosmopolitan
holarctic
Africa
Asia
palaearctic
equivocal
nearctic

Table 2. *Date of divergence (millions of years) for* Taenia saginata *and* T. asiatica *based on estimated cytochrome* c *oxidase I (COI) substitution rates in other taxa*

(The number of third positions in the sampled sequence is denoted by '*n*'. The substitution rate refers to the per-base substitution rate per million years for the pair (i.e. twice the rate for an individual lineage). The estimated number of substitutions separating *T. saginata* and *T. asiatica* is 0.070 per base for 122 third positions (s.e.m. = 0.025). References for COI sequences are as follows: *Mus musculus*, Bibb *et al.* (1981); *Rattus norvegicus*, Gadaleta *et al.* (1989); *Homo sapiens* and *Pan troglodytes*, Horai *et al.* (1992); *Alpheus cylindricus* sp. A and B GenBank accession numbers U02007 and U02008, respectively, from the study of Knowlton *et al.* (1993); *Sphyrna tiburo* Atlantic and Pacific, G. Naylor, unpublished data (used in Martin *et al.* (1992)); and *Sesarma crassipes* and *S. aequatoriale*, European Molecular Biology Laboratory accession numbers AJ225859 and AJ225883, respectively, from the study of Schubart *et al.* (1998). References for absolute divergence dates are as follows: *Mus–Rattus*, Jaeger *et al.* (1986); *Homo–Pan*, WoldeGabriel *et al.* (1994); *Alpheus cylindricus* A–B, *Sesarma crassipes–S. aequatoriale* and *Sphyrna tiburo* Atlantic–Pacific, Knowlton *et al.* (1993).)

taxa	*n*	substitution rate (s.e.m.)	*T. saginata–T. asiatica split* (95% confidence interval)
Mus–Rattus	513	0.078 (0.007)	0.90 (0.22–1.87)
Homo–Pan	513	0.069 (0.008)	1.01 (0.24–2.21)
Alpheus cylindricus A–B	202	0.090 (0.016)	0.78 (0.17–2.02)
Sphyrna tiburo Atlantic–Pacific	37	0.041 (0.022)	1.71 (0.24–∞)
Sesarma crassipes–S. aequatoriale	187	0.072 (0.014)	0.97 (0.21–2.65)

and *Rattus*, an 11-fold faster rate in *Taenia* would give a point estimate of about 90 000 years for the divergence of *T. saginata* and *T. asiatica*, which still pre-dates animal domestication. None the less, the chewing-lice study indicates that extrapolation of substitution rates across taxa may be hazardous.

Without diminishing this problem too much, we would like to point out that extremely rapid substitution rates in mitochondrial DNA are usually associated with either high metabolic rates or short generation times (Martin & Palumbi 1993; Rand 1994). Chewing lice, for example, have a generation time of about 40 days (Hafner *et al.* 1994). *Taenia* have neither high metabolic rates nor short generation times; metabolism is relatively inefficient in tapeworms and generation times for *Taenia* spp. may extend to more than five months for development from oncosphere to cysticercus larvae and adults (e.g. Schmidt & Roberts 1989). The requirements of a complex life cycle, dependent on predator–prey interactions, further lengthens the generation time of taeniid tapeworms. It is also conceivable that a parasitic lifestyle may relax functional constraints on sequence evolution, resulting in relatively rapid substitution rates. It seems unlikely, however, that this would have much effect on the synonymous changes used in our analyses.

(b) *The origins of* Taenia *in humans*

In short, phylogenetic, geographical, ecological and molecular-divergence evidence (the latter for *T. saginata* and *T. asiatica*) suggest that *Taenia* became associated with hominids and the genus *Homo* prior to the origin of modern humans in Africa (Wood 1992; Vrba 1994). The origin of these host–parasite assemblages is attributable to direct predator–prey associations between hominids and bovids or via the scavenging of bovids killed by carnivorous predators including a paleoguild of felids, canids and hyaenids on sub-Saharan African savannah (Lewis 1997). Additionally, divergence of *T. asiatica* may have been a consequence of the dispersal of hominids from Africa with the subsequent isolation of hosts and parasites in Asia. This may provide further corroboration of the relatively long association between *Taenia* and hominids and is consistent with a hypothesis for early dispersal of *Homo* from Africa to Asia (Larick & Ciochon 1996; Gabunia *et al.* 2000).

Emergence of the genus *Homo* has been linked to climatic fluctuations and habitat disruption about 2.5–2.0 Myr ago coinciding with the initial transition of forests to open grassland in Africa (Stanley 1992; Vrba 1994; De Menocal 1995; Larick & Ciochon 1996). A proliferation of savannah-adapted antelopes (Vrba 1985) resulted in diversified food resources for hominid scavengers exploiting bovid prey taken by large felids and hyaenids (Larick & Ciochon 1996; De Heinzelin *et al.* 1999; Sponheimer & Lee-Thorp 1999) (table 1). An omnivorous diet, dependent on scavenging, for pre-human hominids would have promoted sharing of parasites within a guild of carnivores and their bovid prey, thus providing the ecological context for the evolution of *Taenia* specialized in human definitive hosts. The estimated age for the divergence of *T. saginata* and *T. asiatica* is compatible with the acquisition of *Taenia* by hominids coincidental with a shift from a herbivorous to an omnivorous diet (Larick & Ciochon 1996; De Heinzelin *et al.* 1999). The relationships for species of *Taenia* ancestral

Figure 1. (*Opposite*) Phylogenetic relationships and host associations among species of *Taenia*. The tree (a majority rule consensus of 124 most parsimonious trees) is based on analyses of 35 species-level taxa. Species of *Taenia* in human definitive hosts (asterisks) can be divided into two sub-clades: the '*T. solium* sub-clade' containing *T. solium*, *T. hyaenae*, *T. crocutae*, *T. gonyamai* and *T. madoquae*; and the '*T. saginata* sub-clade' including *T. saginata* and its sister species, *T. asiatica* and *T. simbae*. Parsimony mapping was used to examine the putative relationships for *Taenia* spp. and (*a*) definitive hosts, (*b*) primary intermediate hosts and (*c*) geographical range. Not all host families, particularly those shown in the legends for intermediate hosts, are depicted on the trees due to multiple host groups and polymorphic coding in terminals for some species of *Taenia* (i.e. Suidae, Procaviidae, Canidae and Primates for *T. solium*; see also table 1 for context). Equivocal coding, when present in some branches, represents unresolved relationships; polymorphic coding is limited to terminals.

to either *T. solium* or *T. saginata* + *T. asiatica* suggest that antelope were significant components in the diets of *Homo* spp. in the Late Pliocene (table 1; figure 1*b*). Parasitological data reinforce theories about the ecology of hominids in Africa during their diversification in the Late Pliocene and Pleistocene (Vrba 1994; Bromage & Schrenk 1995; De Heinzelin *et al.* 1999).

A clear implication of our analyses is that colonization of hominids and the occurrence of *Taenia* in humans predates the domestication of major food animals and must therefore be decoupled from the domestication of either bovids or suids and from the development of agriculture. The expansion of human agriculture and animal husbandry, however, may have played a later significant role in the global distribution of some species of *Taenia*. In contrast with long-held hypotheses linking the origins of human-specific *Taenia* to animal domestication (Baer 1940; Cameron 1956), it is apparent that cattle and pigs secondarily acquired *Taenia*, which now circulate in synanthropic cycles, from humans.

The acquisition of *Taenia* from humans by species of domestic animals has apparently occurred on at least three separate occasions, represented now by *T. saginata* in cattle and the separate lineages *T. asiatica* and *T. solium* in swine. For *T. solium*, a species with a diverse array of potential intermediate hosts (table 1), it is also suggested that transmission among humans may have been enhanced by cannibalism or the consumption of dogs (Baer 1940). Subsequent to the establishment of life cycles incorporating humans as definitive hosts and domestic animals as obligatory intermediate hosts, natural selection would have resulted in increased specificity of cestodes for these hosts circulating in a synanthropic cycle.

Despres *et al.* (1992) presented evidence regarding the origin of schistosomes in hominids indicating host switching from ruminant and rodent definitive hosts, followed by radiation during the Late Miocene, Pliocene and Early Pleistocene. Their hypothesis suggested the kinds of habitats used by pre-human hominids. Our analyses of the evolution of *Taenia* demonstrate that these parasites can serve as historical ecological indicators of foraging interactions between the direct ancestors of modern humans and the palaeoguild of large carnivores occupying the savannah of Africa in the Pliocene and Pleistocene. Additionally, it is apparent that ecological associations established by hominid ancestors of *Homo sapiens* have had consequences for the distribution of human pathogens and parasites. This work highlights the utility of parasitological data in elucidating the history and behaviour of human ancestors.

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